Great Basin Naturalist 52(4), pp. 328–334

TERRESTRIAL VERTEBRATES OF THE MONO LAKE ISLANDS, CALIFORNIA

Michael L. Morrison[1], William M. Block[2], Joseph R. Jehl, Jr.[3], and Linnea S. Hall[1,4]

ABSTRACT.—We compared vertebrate populations between the two major islands (Paoha and Negit) in Mono Lake, California, and the adjacent mainland to further elucidate the mechanisms underlying island colonization. Deer mice (*Peromyscus maniculatus*) and montane voles (*Microtus montanus*) were captured on Paoha, but only deer mice were captured on Negit. In contrast, eight species of rodents were captured on the mainland. Overall rodent abundance on Paoha and the mainland was similar, but on Negit it was about three times greater than on Paoha or the mainland. Adult deer mice from Paoha were significantly ($P < .05$) smaller in most external body characteristics than mainland mice. Coyotes (*Canis latrans*) and one or two species of lagomorphs were observed on the islands and the mainland. No amphibians or reptiles were found on the islands; both occurred in low numbers on the mainland. Rafting and human transport are probable means of colonization for mice and voles. The occurrence of coyotes on the islands may have modified historic predator-prey relationships, and thus the population of rodents and lagomorphs.

Key words: Mono Lake, islands, colonization, Peromyscus maniculatus, Microtus montanus, *land bridge.*

Island animal populations have attracted much scientific interest because they serve as natural experiments for the study of colonization, dispersal, extinction, competition, and other biological processes (MacArthur and Wilson 1967). Because islands are small and isolated, populations inhabiting them are more vulnerable to stochastic events than their mainland counterparts.

Most previous studies of island zoogeography have emphasized patterns of island occupancy, morphology, and genetics of restricted subsets of the islands' fauna (reviewed by Peltonen and Hanski 1991). Our goals were to compare island and mainland vertebrates of Mono Lake and the surrounding Mono Basin, California, in light of natural and human-influenced processes. This area was of interest because no thorough surveys had been conducted on the islands of this large saline lake, and because of possible changes in local ecology associated with falling lake levels from water diversion for human consumption.

MONO BASIN AND ISLANDS

Mono Basin is the hydrologic drainage basin for Mono Lake. The basin is surrounded by the Sierra Nevada to the west and the Great Basin ranges to the north, east, and south. Mono Lake, estimated at 500,000 years of age, is one of the oldest lakes in North America. Because no water naturally flows out of the basin, and because of long-term evaporation coupled with water diversion, the lake's salinity is about 2.5 times that of the ocean. In October 1986 the surface area of the lake was about 177 km^2 (Mono Basin Ecosystem Study Committee 1987).

There are two major islands in the lake: Paoha Island at about 7.7 km^2 and Negit Island at only about 1.3 km^2 (Fig. 1). Paoha formed from volcanic activity and an uplift of lake sediment some time between 1723 and 1850 A.D. Negit formed as a result of a series of eruptions beginning about 200 A.D. (Mono Basin Ecosystem Study Committee 1987, U.S. Forest Service 1989).

[1]Department of Forestry and Resource Management, University of California, Berkeley, California 94720, and White Mountain Research Station, 3000 E. Line Street, Bishop, California [illegible]
[2]USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Forest Sciences Lab, Tempe, Arizona 85287
[3]Sea World Research Institute, Hubbs Marine Research Center, 1700 South Shores Road, San Diego, California 92109
[4]Present address: School of Renewable Natural Resources, University of Arizona, Tucson, Arizona 85721

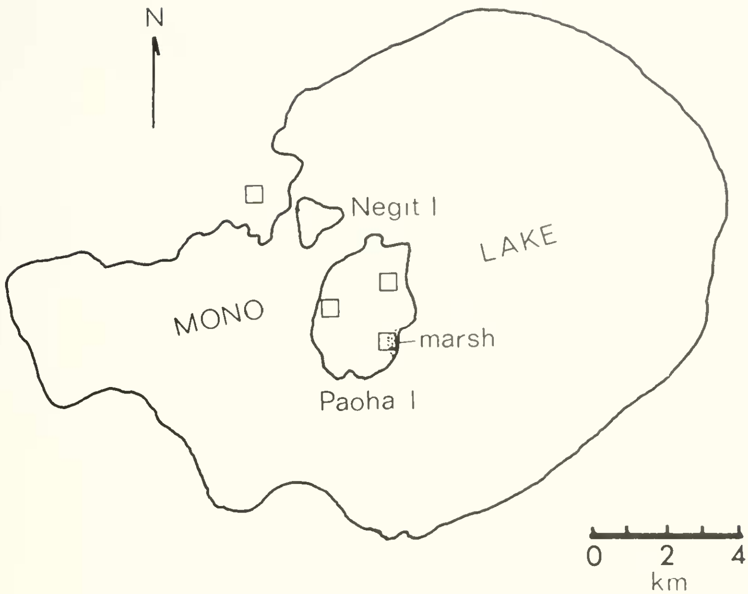

Fig. 1. Mono Lake and the two major islands, Paoha and Negit; small islets are not shown. The boxes indicate the general location of the 1991 study plots; stippling indicates the marsh on Paoha. Redrawn from various U.S. Forest Service maps.

Beginning in 1941 the major streams entering Mono Lake were diverted and their water was transported to Los Angeles, California. This diversion lowered the lake level about 15 m by 1981, to the modern historic low, and also decreased the lake volume by about 50% (Mono Basin Ecosystem Study Committee 1987, Botkin et al. 1988). Although diversions have been halted, a continuing drought (through at least 1992) that began in 1986 has prevented any significant rise in the lake level.

Paoha and Negit islands are located along an axis running perpendicular from the northern shore of Mono Lake, with Paoha the farthest away and about 1 km from Negit. Since its formation, Negit has been separated from the mainland by 0 to >3 km (Mono Basin Ecosystem Study Committee 1987: Figs. 1.3 and 6.1). However, no mainland connection with Negit existed since the formation of Paoha until the late 1970s; the next most recent land bridge apparently occurred about 500 years before present. During our study in 1990–91, Negit was separated from the mainland by several hundred meters of mudflats and a few meters of shallow water; this area is referred to herein as the land bridge.

We know of only two previous small mammal trapping efforts on the islands. In 1975 W. M. Hoffmann (unpublished report) captured no small mammals on Paoha in one night of effort. J. H. Harris (personal communication) captured deer mice (*Peromyscus maniculatus*) on Negit during several days of trapping in the early 1980s. One of us (JRJ) has made repeated visits annually to the islands since 1980, making visual observations, but not trapping. All other accounts of the islands' mammal fauna are from recollections of early settlers and local residents (e.g., Fletcher 1987, personal communication with JRJ).

STUDY AREAS

Paoha Island can be divided into two general vegetative zones: a small (about 2 ha) spring-fed marsh along the southeastern shore, and the remaining nonmarsh vegetation. Vegetation in the marsh is composed of rush (*Juncus effusus*), bullrush (*Scirpus americanus*), saltgrass (*Distichlis spicata*), foxtail (*Hordeum jubatum*), and bassia (*Bassia hyssopifolia*). Nonmarsh areas are dominated by greasewood (*Sarcobatus vermiculatus*) and hopsage (*Grayia spinosa*); sagebrush (*Artemisia tridentata*) is present but rare. Grasses and herbaceous plants are scarce and concentrated in the marsh and one small (about 0.3 ha) grassland site located upslope about 300 m from the marsh. The grassland area is dominated by exotic cheatgrass (*Bromus tectorum*). Negit Island lacks any marsh vegetation and has no permanent freshwater. The upland is similar to Paoha except for more cover by sagebrush. Dominant vegetation on the mainland plots is sagebrush, rabbitbrush (*Chrysothamnus nauseosus*), bitterbrush (*Purshia tridentata*), and scattered individuals of greasewood, curlleaf mahogany (*Cercocarpus ledifolius*), and desert peach (*Prunus andersonii*). Vegetation in the basin was detailed by Burch et al. (1977). Soils are a loose mixture of sand, gravel, ash, and silt (Loeffler 1977).

In 1990 trap lines were established to determine species composition and approximate distributions of small mammals on Paoha and Negit. Specific trap locations were based on ease of boat landing and proximity to the next nearest trapping location; adjacent trap lines were at least 200 m apart.

In 1991 we systematically established 10 fixed study plots (50 × 20 m) on Paoha Island and 5 on the adjacent mainland to compare mammals on the island and mainland; island plots were placed in the marsh (3 plots) and dry shrub vegetation (7 plots). All mainland plots were located to the north and northeast of Black Point on the northwest shore of Mono Lake. This location was selected because its vegetation resembles the dominant vegetation on Paoha Island and represents a likely source for terrestrial animals.

METHODS

Small Mammal Live-Trapping

All traps used during this study were large (7.6 × 8.9 × 22.9 cm [3 × 3.5 × 9 inch]) Sherman live-traps. In 1990 trapping was done on Paoha Island on 27–29 April and 23–25 August, Negit Island on 27–29 April, and the mainland on 4–7 September. Trap spacings ranged from 10 to 20 m and were based on availability of vegetative cover. Traps were baited with rolled oats and peanut butter and checked each morning for 1–3 days depending upon weather conditions and thus access to the islands. Mainland trapping in 1990 was restricted to a marsh on the northern shore of the lake. Captures were identified to species, sex, and age and were measured, marked, and released at the trap location. Measurements between sexes and between island and mainland populations of deer mice were compared using t tests (Zar 1984:126–131).

In 1991, within each plot on Paoha described above, 18 large Sherman live-traps were placed at 10-m spacings (1 row of 6 traps along each long axis of a plot). Each plot was trapped for a total of 54 trap-nights and days (i.e., traps were left open constantly for 3 days and checked both during the morning and in late afternoon). Traps were baited and animals handled as in 1990. Mainland and Paoha traps were run 7 May–24 June. Trap lines were run on Negit 4–5 August, as described for 1990. Data are reported here as the number of new individuals (i.e., excluding recaptures) captured per 100 trap-nights; we assume that this measure of capture success is an adequate index of actual population abundance. Indices of abundance were compared using chi-square goodness of fit (Zar 1984:40–43).

Other Surveys

During 1991, one 4.2-L (1-gal) can was placed near the center of each trapping plot. Cans were placed on all mainland plots and on six Paoha Island plots. Each was covered with a wooden board raised 2–3 cm above the can. Traps were run 4–17 days. Three additional traps were placed in the marsh on the southeast side of Paoha Island, this being the most likely location for shrews (Soricidae). Thus, six traps were placed in the marsh. All mainland pitfalls were opened 9–12 June; island traps were opened 7 May–4 June.

A 1-m^2 area in an open location near the center of each plot was selected to determine the presence of medium- to larger-sized mammals traveling across the plot. The soil in a track plot was smoothed by hand and moistened with water; fine-grained sand or soil was added as needed. A can of chicken-flavored cat food was secured at the center of each track plot. Each plot was checked daily for three days for evidence of wildlife use. One-half of the study plots on Paoha and three mainland study plots were used.

Time-constraint surveys of one-person-hour duration each were conducted in all study plots. The species, date, time, location, and general vegetation type for each observation were recorded.

Museum Records

We obtained records for all vertebrates collected in Mono Basin from the Los Angeles

TABLE 1. Index of abundance (no./100 trap-nights) for small mammals captured on study plots on Paoha Island (n = 10 plots) and adjacent mainland (n = 5 plots), and on Negit Island (trap lines), Mono Basin, California, 1991.[a]

Species	Paoha Island (trap-nights)				
	Total marsh (108)	Total nonmarsh (324)	Total island (432)	Negit Island (120)	Total mainland (342)
Peromyscus maniculatus	17.6	13.0	14.1	62.5	6.4
Male	8.3	9.0	8.8	32.5	4.1
Female	9.3	4.0	5.3	30.0	2.3
Microtus montanus	5.6	0.9	2.1		0.3
Perognathus parvus					6.7
Dipodomys panamintinus					5.3
D. microps					1.8
Peromyscus boylii					0.3
Eutamius minimus					0.3
Spermophilus beecheyi					0.3
Total	23.2	13.9	16.2	62.5	21.3

[a]Chi-square analysis: all comparisons between total marsh and total nonmarsh on Paoha $P > .05$; between Paoha total island and Negit Island $P < .001$, between total Paoha and total mainland $P > .05$; and between total mainland and Negit $P < .01$

County Museum of Natural History (LACMNH) and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ). Although no records were available for the islands, data from the basin were summarized to supplement published accounts of mainland vertebrate surveys. Voucher specimens were deposited at the MVZ.

RESULTS

Small Mammal Trapping

Only deer mice and montane voles (*Microtus montanus*) were captured on Paoha Island. Most voles were captured in the marsh; deer mice were also slightly more abundant there than in dry shrub plots, but these differences were not significant ($P > .1$). The sex ratio of deer mice was skewed toward males in the dry shrub, but was about even in the marsh (Table 1).

Only deer mice were captured on Negit Island. Mouse abundance was about 4.5 times higher on Negit than on Paoha ($P < .05$), and sex ratios were about even (Table 1).

Eight species of small mammals were captured on the mainland plots in 1991. Great Basin pocket mice (*Perognathus parvus*), deer mice, and Panamint kangaroo rats (*Dipodomys panamintinus*) had similar relative abundances and were the only species with abundances >5 individuals/100 trap-nights). Except for the Great Basin kangaroo rat (*Dipodomys microps*), all species were captured rarely (all at 0.3 animals/100 trap-nights). Overall abundance of small mammals on Paoha was similar to that on the mainland, but on Negit it was almost three times greater than that on Paoha ($P < .001$) or the mainland ($P < .01$; Table 1).

Abundance of deer mice approximately doubled ($P < .01$) on Paoha between April (early breeding) and August (end of breeding) 1990. Subadult males accounted for 67% of this increase (Table 2), while subadult females accounted for only 6%. Total male and female abundance was about equal in April; the number of males caught increased by 63% and females only by 35% in August, although the difference was not significant ($P > .1$).

Male and female abundances of deer mice were similar on Negit in April 1990; no comparable August data were available. Total abundance on Negit in April was 48% higher ($P < .05$) than that on Paoha (Table 2).

Adult male deer mice from Paoha weighed significantly less and had significantly shorter tails, feet, and tail:body-length ratios than mainland animals; body and ear lengths were not different (Table 3). Adult females from Paoha were significantly less heavy than mainland animals and had smaller but not significantly different average measurements for other characters. Comparisons with Negit mice were not possible because an insufficient number of animals were measured.

Other Surveys

ISLANDS.—The six pitfalls in the Paoha marsh were run for 13 days (78 trap-days) and captured 7.7 voles/100 pitfall-days; the three

TABLE 2. Abundance (no./100 trap-nights) of *Peromyscus maniculatus* on Paoha and Negit islands, Mono Lake, California, 1990.

	Paoha Island		Negit Island
	April	August	April
Trap-nights	290	160	74
Male			
Adult	7.6	8.8	13.5
Subadult	1.0	15.0***	0.0
Juvenile	0.7	1.3	0.0
Total	9.3	25.0**	13.5
Female			
Adult	5.9	8.1	10.8
Subadult	3.8	5.0	4.1
Juvenile	0.0	1.9	0.0
Total	9.7	15.0	14.9
Overall	19.0	40.0**	36.5**

Chi-square analysis: **$P < .01$, ***$P < .001$, Paoha April vs. August and Paoha April vs. Negit April.

pitfalls in the dry shrub were run for 17 days (51 pitfall-days); no animals were captured. Track plots were run for 3 days on Paoha, resulting in a total effort of 15 track-plot-days. One set of coyote (*Canis latrans*) tracks was found on a plot in the marsh, and one set of unidentified rodent tracks (likely deer mouse) was found on a dry shrub plot. Coyote tracks and scat were seen throughout both islands; they were especially evident on the southeast end of Paoha, including the marsh. Black-tailed jackrabbits (*Lepus californicus*) were uncommon but were seen occasionally on both islands. Cottontails (*Sylvilagus* spp.) were seen rarely on Negit but were not evident on Paoha. Rabbit pellets were conspicuous on the islands, indicating that the populations had been greater at a previous time. No herps were observed on either island during any survey, or in any yearly island visit by JRJ since 1980. Scattered individuals of sagebrush lizard (*Sceloporus gracious*) were seen while walking on and near the mainland study plots.

MAINLAND.—The five pitfalls were run for 4 days (20 pitfall-days). Four sagebrush lizards were captured (20 lizards/100 pitfall-days). Track plots were run for a total of 3 days on three study plots, with one set of black-tailed jackrabbit, two sets of kangaroo rat (species unknown), and one set of unidentified small rodent tracks observed. Thus, there were four separate animals in 9 track-plot-days. Coyote tracks were seen on the plots and coyotes were heard calling adjacent to plots. Numerous rabbit and kangaroo rat tracks were present on all plots; cottontails were also seen adjacent to the plots on several occasions.

DISCUSSION

Only two species of small mammal (deer mouse and montane vole) were trapped on Paoha, and one species (deer mouse) on Negit, compared with eight species—including deer mice and montane voles—on the adjacent mainland. Visual and track surveys found the jackrabbit, cottontail, and coyote on Negit Island and the mainland; all but the cottontail were evident on Paoha. In contrast, at least 20 species of small mammals have been observed around the shores of Mono Lake (Harris 1982, 1984). In addition, weasels (*Mustela* spp.), badger (*Taxidea taxus*), bobcat (*Lynx rufus*), mountain lion (*Felis concolor*), black bear (*Ursus americanus*), and mule deer (*Odocoileus hemionus*) occur around Mono Lake (Harris 1982). Furthermore, lion remains have been reported from an islet near Negit and from the vicinity of the Negit-mainland land bridge (Mono Lake Committee, unpublished observation). The presence of montane voles on Paoha was associated with the marsh and grass vegetation that is absent on Negit. The current lake level has allowed the Paoha marsh to expand onto an exposed lake shelf, thus increasing potential vole habitat. The environment may be unsuitable on the islands for persistence of the larger carnivores and deer but appears suitable on Paoha (because of water and rodents) for weasels and possibly badgers.

Animals can colonize islands by swimming, rafting, using ice bridges, being inadvertent passengers on watercraft (Calhoun and Greenbaum 1991), intentional or unintentional releases, or by flying; all but flying may apply to the animals discussed herein. The lack of historic, quantitative data, however, prevents determination of the method(s) and date(s) of arrival of animals on the Mono Lake islands. However, Hoffman (unpublished report) set 76 Sherman traps for one night (24 May) in 1974 in various locations, including in and around the same marsh and grassland areas we trapped. He caught no animals but did locate a rodent faex. Although Hoffman's efforts were minimal, his data at least indicate the presence of rodents prior to 1974.

Although the earliest historic accounts of local Native Americans date to the early 1860s (Jehl et al. 1984, 1988), various peoples are

TABLE 3. Characteristics of adult *Peromyscus maniculatus* captured on Paoha Island, Mono Lake, and adjacent mainland during 1990 and 1991.

	Adult male[a]				Adult female[b]			
	Paoha		Mainland		Paoha		Mainland	
Characteristic	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Mass (g)[c]	17.2	2.11	18.8	1.29**	18.1	2.29	19.9	2.80
Body length (mm)	81.4	5.13	81.4	2.87	79.4	6.50	81.1	3.18
Tail length (mm)	64.5	4.32	67.1	5.34*	66.4	6.85	69.1	6.34
Foot (mm)	20.0	1.07	20.9	0.95**	20.0	0.91	20.6	1.08
Ear (mm)	17.4	1.08	17.4	1.45	17.4	1.04	17.9	1.38
Tail/body	0.79	0.06	0.82	0.07*	0.84	0.07	0.85	0.07

[a]Sample size = 50 individuals each area, except for mass
[b]Sample size = 15 individuals each area, except for mass
[c]Excludes pregnant females. Paoha $n = 12$, mainland $n = 13$
*$P < .05$ **$P < .01$, t test

thought to have visited the basin for a much longer period (Fletcher 1987). Western immigrants began making trips to the islands by the 1860s (Jehl et al. 1984, 1988, Fletcher 1987). A chicken (*Gallus gallus*) and domestic lagomorph ranch was established on Paoha in the late 1870s, a domestic goat (*Capra* sp.) ranch was initiated in the 1890s (Fletcher 1987), and a mineral salts and health spa venture was attempted in the 1940s. Lagomorphs raised commercially were apparently European hares (*Lepus* sp.), but there is no evidence that these hares remained on Paoha after the early 1920s when the commercial operation ceased. A few goats survived on Paoha until at least 1975 (Hoffman, unpublished report) but were extirpated by 1980.

Thus, human movements onto the islands were frequent, and rodents, such as deer mice and voles, could have been inadvertently transported in the grain, hay, and other items taken to support activities on the islands. We do not know if native lagomorphs were tranported to the islands by humans.

There is debate in the literature over the abilities of *Peromyscus*, *Microtus*, and other small mammals to colonize islands by swimming or rafting because they are not well adapted for exposure to water (Redfield 1976, Calhoun and Greenbaum 1991, Peltonen and Hanski 1991). We have no direct way of quantifying the relative probabilities of inadvertent human transport versus rafting. However, the known and frequent history of human visitation and habitation for commercial purposes during this century results in a higher frequency of occurrence and less harsh means of possible transport than does rafting due to flooding events. Confounding the present situation is the land bridge or near land bridge. Movement across the land bridge to Negit, followed by swimming or rafting to Paoha, is likely more probable now than historically.

The absence of lizards on the islands is perplexing, however, as there appears to be ample habitat on the islands, and species on the mainland are potentially good colonizers (*sensu* Case 1975, 1983). However, mainland populations are small, as the elevation of the Mono Basin is at the upper end of the normal range for reptiles in the Sierra Nevada (summarized from Storer and Usinger 1968). Therefore, their chance of arrival and persistence is low.

Snakes (*Pituophis melanoleucus* and *Thamnophis elegans*) and amphibians (*Bufo boreas*, *Hyla regilla*, *Scaphiopus hammondii*, *S. intermontanus*) are found around Mono Lake (MVZ specimens, personal observation), but they are scarce locally (personal observation). There are no historic records of snakes or amphibians on either island, and we saw no evidence of either during our visits. As discussed above for lizards, it appears that the chance of arrival and persistence of snakes and amphibians is low.

The Mono Lake islands parallel other islands in having a greater population abundance (especially Negit) and a simple species composition relative to the mainland. Larger relative abundances may be because few predators are present and the lack of nonavian food competitors, as has been postulated for other island rodent populations (e.g., Halpin and Sullivan 1978). The few rodent species, absence of lizards, and reduced bird-species richness (Hall et al., in preparation) on the islands may result in density compensation (*sensu* MacArthur et al. 1972, Case 1975) by the islands' *Peromyscus* populations.

In contrast to island biogeographic theory (Redfield 1976, Sullivan 1977), deer mice are smaller on the islands than on the mainland. Although a founder effect (*sensu* Kilpatrick 1981, Calhoun and Greenbaum 1991) could have resulted in smaller individuals on the islands than on the mainland, there is likely some combination of ecological factors on the Mono Lake islands that has either resulted in maintenance of small body size or has directed selection toward smaller body size. In our study the sex ratio of deer mice appears to be male biased, although more intensive trapping, both within and between years, would be necessary for confirmation because of potential trapping biases associated with dispersing young males.

ACKNOWLEDGMENTS

We thank Paul Aigner, Jean Block, Martin Morton, and Paul Stapp for assistance with fieldwork; Edward Beedy for helping with study design; John Harris and several anonymous referees for reviewing earlier drafts; and Lorraine Merkle for manuscript preparation. Data collection was supported by subconsultant contract to Jones and Stokes Associates, consultant to Los Angeles Department of Water and Power and California State Water Resources Control Board; and the White Mountain Research Station, University of California, Los Angeles.

LITERATURE CITED

BOTKIN, D., W. S. BROECKER, L. G. EVERETT, J. SHAPIRO, AND J. A. WIENS. 1988. The future of Mono Lake. University of California, Water Resources Center, Report No. 68. Berkeley, California. 29 pp.

BURCH, J. B., J. ROBBINS, AND T. WAINWRIGHT. 1977. Pages 114–142 *in* D. W. Winkler, ed., An ecological study of Mono Lake, California. University of California, Institute of Ecology Publication No. 12. Davis, California.

CALHOUN, S. W., AND I. F. GREENBAUM. 1991. Evolutionary implications of genetic variation among insular populations of *Peromyscus maniculatus* and *Peromyscus oreas*. Journal of Mammalogy 72: 248–262.

CASE, T. J. 1975. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. Ecology 56: 3–18.

______. 1983. Niche overlap and the assembly of island lizard communities. Oikos 41: 427–433.

FLETCHER, T. C. 1987. Paiute, prospector, pioneer: a history of the Bodie–Mono Lake area in the nineteenth century. Artemisia Press, Lee Vining, California. 123 pp.

HALPIN, Z. T., AND T. P. SULLIVAN. 1978. Social interactions in island populations of the deer mouse, *Peromyscus maniculatus*. Journal of Mammalogy 59: 395–401.

HARRIS, J. H. 1982. Mammals of the Mono Lake–Tioga Pass region. Kutsavi Books, Lee Vining, California. 55 pp.

______. 1984. An experimental analysis of desert rodent foraging ecology. Ecology 65: 1579–1584.

JEHL, J. R., JR., D. E. BABB, AND D. M. POWER. 1984. History of the California Gull colony at Mono Lake, California. Colonial Waterbirds 7: 94–104.

______. 1988. On the interpretation of historical data, with reference to the California Gull colony at Mono Lake, California. Colonial Waterbirds 11: 322–327.

KILPATRICK, C. W. 1981. Genetic structure of insular populations. Pages 28–59 *in* M. H. Smith and J. Joule, eds., Mammalian population genetics. University of Georgia Press, Athens.

LOEFFLER, R. M. 1977. Geology and hydrology. Pages 6–38 *in* D. W. Winkler, ed., An ecological study of Mono Lake, California. University of California, Institute of Ecology Publication No. 12. Davis, California.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey. 203 pp.

MACARTHUR, R. H., J. M. DIAMOND, AND J. R. KARR. 1972. Density compensation in island faunas. Ecology 53: 330–342.

MONO BASIN ECOSYSTEM STUDY COMMITTEE. 1987. The Mono Basin ecosystem: effects of changing lake level. National Academy Press, Washington, D.C. 272 pp.

PELTONEN, A., AND I. HANSKI. 1991. Patterns of island occupancy explained by colonization and extinction rates in shrews. Ecology 72: 1698–1708.

REDFIELD, J. A. 1976. Distribution, abundance, size, and genetic variation of *Peromyscus maniculatus* on the gulf islands of British Columbia. Canadian Journal of Zoology 54: 463–474.

STORER, T. I., AND R. L. USINGER. 1968. Sierra Nevada natural history. University of California Press, Berkeley. 374 pp.

SULLIVAN, T. P. 1977. Demography and dispersal in island and mainland populations of the deer mouse, *Peromyscus maniculatus*. Ecology 58: 964–978.

U.S. FOREST SERVICE. 1989. Mono Basin National Forest Scenic Area, comprehensive management plan. USDA Forest Service, Inyo National Forest, Bishop, California. 95 pp.

ZAR, J. H. 1984. Biostatistical analysis. 2nd edition. Prentice-Hall, Englewood Cliffs, New Jersey. 718 pp.

Received 19 February 1992
Accepted 1 October 1992